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SIZE INHERITANCE AND GROWTH IN A MOUSE SPECIES CROSS (*MUS MUSCULUS* × *MUS BACTRIANUS*)

III. INHERITANCE OF ADULT QUANTITATIVE CHARACTERS¹

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FOUR FIGURES

Although the multiple-factor theory is now held by the majority of investigators in quantitative genetics, there is, however, an increasing minority which a purely genetic interpretation does not satisfy. Sumner ('23, '23 a), on the basis of his extensive experiments in hybridizing subspecies of *Peromyscus*, rejected the multiple-factor hypothesis as a satisfactory explanation for the inheritance of quantitative differences. Although he found the F_2 generation preponderantly tending to be more variable than the F_1 , he did not believe that this condition was necessarily produced by the recombination of numerous size factors. The sinistrodextral ratios of paired bones were consistently more variable in the F_2 generation, notwithstanding that these ratios, he states, are known not to be hereditary at all. Admitting this, the suitability of the multiple-factor hypothesis is, to say the least, impaired.

Castle ('29), reporting the results of his comprehensive investigations on size inheritance in rabbits, sums up his present views on the subject as follows:

¹One of a series from a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Zoölogy of the University of Michigan.

It is an open question whether the general rate of growth, which influences the size of the organism as a whole without influencing its proportions except as these are dependent on total size, is a matter of inheritance through genes located in the chromosomes. There is no *a priori* reason why general body size should not be thought capable of being influenced by chromosomal genes since external conditions and even pathological conditions within the organism are known to influence it. But the evidence for such a view is as yet entirely lacking.

The genes for the sharply discontinuous characters—the so-called qualitative characters—may in addition to their qualitative action have a quantitative effect as well. The effect of the factor for pink-eye on the coat color of rodents is well known. There are several other cases in which the effects are still more striking and apparently more unrelated.

De Aberle ('27) showed that mice of the genetic composition WW are anemic, thus explaining the lethal action of the gene for dominant spotting in the homozygous condition. The blood of newborn anemic mice contained only 25 per cent as much hemoglobin and 14 per cent as many red blood cells as normal young. Danforth ('27) found the gene producing a pronounced form of adiposity in mice to be identical with the one responsible for yellow coat color (A^y). These mice weighed about twice as much as mice of other colors. Since no cross-overs whatsoever were observed, Danforth considered the genes to be identical rather than merely closely linked. Little ('17) had previously demonstrated the genetically independent lethal effects of the genes (when homozygous) for dominant spotting (W) and yellow coat color (A^y).

INVESTIGATIONS ON SIZE INHERITANCE

Emerson and East ('13) made a detailed study of the inheritance of numerous quantitative characters in maize. Among these were number of rows per ear, ear length, ear diameter, weight of seeds, breadth of seeds, height of plants, number of nodes, number of stalks per plant, and earliness in maturing. Except for a few instances in which heterosis

obscured the results, the F_1 generation was intermediate for almost every character studied. (In one type of mating a twelve-rowed ear was dominant over an eight-rowed.) The F_2 generation uniformly exhibited a greater range than the F_1 , in some cases even exceeding the parental extremes. The results obtained are easily explicable by the assumption of multiple factors.

Lindstrom ('29), in an investigation of linkage in maize, found the F_1 generation intermediate in number of rows of seeds per ear. Twelve-rowed varieties crossed with eight-rowed varieties gave ten-rowed progeny; sixteen-rowed $\times$ eight-rowed gave twelve-rowed, etc. The back-cross generations were likewise more or less intermediate between the F_1 and the parental form.

Although maize has been investigated most extensively, other plants, including the genera *Lycopersicum*, *Nicotiana*, and *Phaseolus*, have received considerable attention. In general, the results are comparable with those obtained in maize.

Phillips ('12, '14) crossed English mallard ducks with French Rouens, a breed more than twice as large. The characters considered included total weight, as well as measurements of bill, tarsus, neck, and total length. The F_1 generation showed slight variation, all members hovering closely about the midparental value. There was much greater variability among the F_2 's, although in no case did it extend beyond the grandparental race. This increased variability he considered to be due to a partial segregation of multiple genes, or, perhaps, to a modification of the gametes in other ways as a result of their associations in the F_1 zygotes. He concluded that the possibility of the existence of any large and clear-cut size units in birds which would result in an easily recognized numerical ratio in the second hybrid generation was slight.

Goldschmidt ('13), having very small numbers, confirmed Phillips in finding that F_1 ducks were intermediate in weight between the two parental races.

Punnett and Bailey ('14), working with chickens, obtained results indicating a situation quite different from that which Phillips found prevailing in ducks. They concluded that one breed, Gold pencilled Hamburgs, contributed three factors, two of which had greater value than the third, for size; while the other breed, Silver Sebright bantams, introduced one factor. This equaled in potency the third factor of the larger race. Since the factors involved were so few, fairly definite numerical ratios as well as occasional extreme segregates were obtained in the F_2 generation.

Warren ('27) mated White Leghorn fowls with a very large breed, Jersey Black Giants. The mature weight of the F_1 's was intermediate, although approaching the heavier breed. The shank length, on the contrary, was more nearly like that of the Leghorn.

Kopeć ('27), also investigating quantitative characters in fowls, found the F_2 's more variable than the F_1 's in body weight, feather weight, and numerous body form indices.

The genetics of quantitative inheritance has been studied more thoroughly in rabbits than in any other animal. Castle ('09) considered weight, ear length, and bone length probably to be blending in inheritance.

MacDowell ('14) continued this work, devoting especial attention to skeletal measurements. His data showed the existence of a greater variability in both bone lengths and body weight in the F_2 and equally in the back-cross than in the F_1 generation. The F_1 animals were intermediate for all characters.

Punnett and Bailey ('18) crossed large and small breeds of rabbits. The F_1 individuals were intermediate in weight, while the F_2 's were more variable, some approaching the smaller race. The authors believed that size and early maturity were to some extent transmitted independently.

Size inheritance in rabbit crosses was again reported on by Castle ('22). The size characters studied were body weight, ear length, and several bone measurements. The F_1 rabbits were intermediate, although the influence of heterosis raised

the value of the means beyond what they would otherwise have been. When this influence was lost in the F_2 generation, the means sank back to a strictly intermediate position. This generation was more variable than the F_1 . The inheritance, he held, could be correctly described as blending and was in accord with the multiple-factor hypothesis. An attempt was made to estimate statistically the number of different chromosomes (or linkage systems) concerned and it seemed probable that all chromosomes were concerned in size inheritance. No evidence of linkage of size with any of several qualitative characters could be detected.

Pease ('28) published his results on experiments on the inheritance of weight in rabbits. His findings were in agreement with those of previous workers, excepting that the intermediate F_1 's showed no signs of hybrid vigor. His numbers were insufficient to determine whether there was a single predominating weight factor.

In his most recent report on this subject, Castle ('29), as previously stated, concluded that it was an open question whether general size inheritance is a matter of inheritance through chromosomal genes. He had been unable to obtain any crucial evidence for this during his years of investigations on rabbits.

Guinea-pigs appear to be less favorable material for the study of size inheritance. Detlefsen ('14) crossed a small wild cavy (*Cavia rufescens*) with domestic guinea-pigs. The first hybrid generation, probably as a result of heterosis, consisted of animals larger than either parent race. Back-crosses to the guinea-pig failed to reveal any evidence of the segregation of size factors. There was remarkably little variation in either of the parental species, the F_1 , or the back-cross generations. The numbers involved were, however, for the most part, too few to make the study conclusive.

Livesay ('30) studied hybrid vigor in rats (*Rattus norvegicus*). The F_1 animals obtained from crossing inbred strains were distinctly larger than either parent race and were less variable in weight. The F_2 individuals were smaller

than the F_1 and more variable, but less variable than the parent races. Although he obtained no definite evidence for the linkage of growth genes with any of the three qualitative genes studied, he concluded that the difference in size of the rats of the heavy and light groups of the F_2 generation must be due to hereditary size genes probably located on the unstudied chromosomes.

Subspecific crosses in the genus *Peromyscus* were discussed by Sumner ('23, '23 a). Most of the size indices investigated were intermediate in both the F_1 and the F_2 generations, the latter showing a tendency toward an increase in variability.

Gates ('26) found the F_1 hybrids of Japanese waltzing mice (*Mus bactrianus*?) and domestic mice (*Mus musculus*) exhibiting heterosis to a marked degree. In skull length, for example, they far exceeded, and in body weight equaled, the larger parent. In other dimensions, including the number of caudal vertebrae and tail length, they were intermediate.

Little ('27, '27 a), in preliminary reports on the *Mus musculus* $\times$ *Mus bactrianus* cross, stated that hybrids were intermediate in size.

In general, the results of size inheritance investigations have shown the F_1 generation to be intermediate when not augmented by heterosis. The F_2 individuals are likewise intermediate, but usually more variable than the F_1 's. These observations, although not conclusively proving it, are favorable to a mendelian interpretation of the inheritance of quantitative characters on the basis of multiple factors.

ALTERNATIVE INHERITANCE OF SIZE

As in the example cited above, the inheritance of quantitative characters is usually of the type known as blending and characterized by the absence of dominance. There are, however, a number of instances in which the contrasting characters segregate in the ordinary mendelian manner. Belling ('15) reported that a single dominant factor was responsible for the main difference between short and long pods in beans. There were in addition minor factors without dominance

which modified pod length. Davenport ('17) concluded that the factors producing tallness in humans were mostly recessive. Lynch ('21) found short ears in mice to be due to a single recessive autosomal gene. Lindstrom ('26) presented data indicating that in certain tomato crosses small size of the fruit is incompletely dominant. These cases, nevertheless, should be considered as exceptional. They relate, moreover, not to the general size of the organism, but to that of particular parts of it.

HETEROSIS

The question of hybrid vigor, a common phenomenon of interspecific and interracial crosses, has been well summarized by Wright ('22 a) and by Livesay ('30). Two widely held hypotheses have been advanced in explanation. One interpretation holds that hybrid vigor results from the union of unlike elements, a genic dissimilarity, and that the increased heterozygosity per se accounts for the increased vigor of the zygote. The other theory supposes that an increase in the number of special dominant genes—a condition necessarily produced by the union of two widely different gametes—brings about an augmented vigor in the resulting organism. As Wright has pointed out, recessive genes are usually more deleterious than their dominant allelomorphs, so any condition tending to reduce the number of homozygous recessive-factor pairs would add strength. The second theory reduces the matter to a purely genetic basis and is now more generally accepted.

TESTS FOR GENE INHERITANCE OF QUANTITATIVE CHARACTERS

If the multiple-factor hypothesis provides the correct explanation for the mechanism of size inheritance, the F_1 generation should as a rule be intermediate between the parental strains. The F_2 generation should likewise be intermediate for the most part, but exhibiting more variability than the F_1 . Extreme segregates could be expected only when the postulated factors are few in number. These conditions, as we have seen, generally prevail.

Such observations, however, do not definitely prove that size inheritance occurs through chromosomal genes. To determine this point conclusively, linkage between quantitative characters and known qualitative characters must be demonstrated. The likelihood that genes for size are distributed on several or all the chromosomes does not preclude the possibility of the existence of major size genes located at a few definite loci. Were the presence of such determined, the universality of mendelian heredity would be more firmly established.

Such linkage has been found in several forms. In *Lycopersicum*, Lindstrom ('26, '28) has presented evidence indicating that size genes occur in all three main linkage groups. He observed a marked correlation between size of fruit and color of skin and flesh as well as between size of fruit and pubescence. The same author ('29) showed that number of rows in the maize ear, a quantitative character, was associated in inheritance with several simple mendelizing qualitative characters such as cob color, endosperm color, and endosperm texture.

Sax ('23, '24) found pattern of seed coat in beans to be linked with seed weight. In radishes (*Raphanus*) root size is rather closely linked with root color (Frost, '23).

Some evidence has been presented for similar phenomena in animals. Gates ('27) has shown linkage between short ear and dilute pigmentation in the house mouse. This quantitative character, however, like most of those discussed in the preceding paragraphs, affects a definite part of the organism and the inheritance is of the discontinuous type rather than blending.

For the blending type the evidence has thus far been quite uniformly negative in mammals. Castle ('22, '29) could find no evidence in rabbits for the association in inheritance of size with any of several simple qualitative characters affecting coat color.

Livesay ('30) detected no evidence that factors determining body weight in rats were linked with any of three genes

affecting coat color (hooding, color, and agouti). Gates ('26), in his Japanese waltzing mouse (*Mus bactrianus*?) $\times$ house mouse (*Mus musculus*) crosses, selected at random six young (sex not stated) of each of the parental types from the F_2 generation. At the age of sixty days they were killed and several measurements, including skull length, skull width, body length, and tail length, showed that the extracted young deviated consistently in the direction of their respective parental types. Needless to say, the numbers leave much to be desired. At best, the results might indicate the formation of association systems of chromosomes (as Gates believed) rather than linkage of quantitative and qualitative characters.

MATERIAL AND METHODS

The *Mus musculus* animals used in these experiments were obtained from Dr. C. C. Little's inbred strain of dilute brown mice. These mice have been inbred, chiefly by brother-to-sister matings, since 1909 and thus represent a highly homogeneous stock.

The *Mus bactrianus* mice were descendants of animals captured near Peiping, China, and brought to the United States in 1926 by Dr. Sheo Nan Cheer. Since that time they have been mated brother to sister whenever possible, but obviously have not yet approached the degree of genetic homozygosity attained by the race of dilute browns.

Our mice of the species *musculus* are triple recessives in coat color, possessing the genes for dilute pigmentation (d), brown color (b), and non-agouti (a) pattern of the hair. Mouse Club symbols (Cuénot, '28) are used. They are large, long-tailed murids, the average adult having a body weight in excess of 30 grams. The average total length is about 190 mm., of which the tail constitutes approximately 49 per cent. The mean number of caudal vertebrae is twenty-five.

Examples of our Chinese species were identified by Dr. G. M. Allen, of the Museum of Comparative Zoölogy at Harvard University, as *Mus bactrianus* Blyth. Our strain

is intermediate between the subspecies *Mus bactrianus tantillus* Allen and *Mus bactrianus gansuensis* Satunin—on the whole, according to Allen, probably nearer the latter form.

The subspecies, *tantillus*, is described by Allen ('27) as follows:

Tail nearly or quite equalling head and body (averaging 49% of total length); hairs of belly dark-based, tipped with white; throat buffy.

Above, the color is sandy, resulting from a mixture of buffy-tipped with black hairs, the latter more numerous over the rump, giving a slightly darker effect mid-dorsally. Sides clearer buffy. Lower surfaces with the hairs gray-based, tipped with white. Throat with a buffy color. A suffusion of buffy may extend to most of the under surfaces. Ears dusky. Feet dusky, the toes whitish; tail indistinctly bicolor. Mammae 3-2 = 10.

The same author characterizes *gansuensis* as—

. . . . a pallid short-tailed race characteristic of the desert country from eastern Mongolia south-westward across northern Shansi to Kansu. . . . The dorsal color is a pale sandy buff, not darkened medially, the lower surfaces and feet are pure white to the roots of the hairs, and the tail is indistinctly bicolor. The measurements given for the type of *gansuensis* (from Tschortentan, Kansu) indicate a tail 42% of the total length.

Our *bactrianus* exhibit considerable variation in dorsal and ventral coloration. Although the majority are light sandy above, a few, especially young individuals, have a tendency to be darker middorsally. Again, while most have the hairs of the ventral region white to the roots, some individuals are faintly gray-based or even buffy-tinged. A buffy collar may or may not be present.

Mice of our strain, regardless of slight individual variations in coloration, possess the dominant genes affecting coat color for intense pigmentation (D), black color (B), and agouti hair pattern (A). The average adult body weight is about 14 or 15 grams, while the total length is less than 150 mm. The tail averages about 46 per cent of the total length, intermediate between typical *tantillus* and *gansuensis*, but relatively short as compared with our *musculus*. The most usual number of caudal vertebrae is twenty.

It seems quite probable that some variety of this species represents the ancestral stock from which the tame Japanese waltzing mouse is derived. Gates ('26) has summarized the evidence on this point and regards *Mus wagneri* (bactrianus), and not *Mus musculus*, as the ancestral form of the pure Japanese waltzer.

All of the animals have been kept under similar conditions of diet and housing, in order that environmental differences might be eliminated in so far as this is possible. The diet has been constant and consisted of fresh milk daily, with Spratt's dog cakes and hemp and canary seed always available. In addition, fresh lettuce was given once a week. Such a diet has proved eminently suitable for mice.

The animal rooms were well ventilated and maintained at an approximately uniform temperature. One male and several females (usually five or six) were kept in breeding pens $15 \times 12 \times 12$ inches. When observed to be pregnant, a female was removed to a separate pen $12 \times 6 \times 6$ inches, where she was allowed to bear and rear her young to weaning age, thirty-one days. At weaning the sexes were separated and the young animals placed in pens $7\frac{1}{2} \times 12 \times 15$ inches. The number in each pen was rarely more than six, so there was no serious overcrowding. The mice were left in these pens, unless used for breeding, until six months of age, when they were killed.

In addition to general observations on the phenomena attending species crossing, our material is well suited for the detection of linkage between qualitative and quantitative characters. As before mentioned, the two parent species differ markedly in size, *Mus musculus* weighing twice as much as *Mus bactrianus*. They also differ in three freely segregating qualitative factors affecting coat color. An especial advantage lies in the fact that the large species possesses the recessive qualitative genes, while the small form exhibits their dominant allelomorphs. Thus, any tendency of the back-cross phenotypes to vary in the direction of their respective parental types cannot be attributed to invigorating effects which may be inherent in dominant genes.

The characters selected as quantitative indices were: body length, tail length, relative tail length (per cent of total length), number of caudal vertebrae, adult weight, skull length, skull width, humerus length, femur length, and tibia length. With the exception of the number of caudal vertebrae, no records of these characters from animals less than 180 days of age were included in the computations. This precaution was taken to insure the inclusion of only those individuals which had attained approximately their final size.

Brody, Sparrow, and Kibler ('26) state that 98 per cent of the adult weight of the male white mouse is attained in about 5.5 months; of the unmated female, in 6.7 months. Stieve ('23) presents data showing that male mice reach their final growth in twenty to twenty-four weeks.

Bone lengths appear to be favorable characters for the study of size. Schneider and Dunn ('24) observed that bone length was but one-third to one-sixth as variable as body weight in poultry. Dunn ('28) investigated the effect of inbreeding on the bones of the fowl and considers relatively small differences in bone length due to genetic factors. Even slight differences are under a fairly exact hereditary control and sufficiently insulated from environmental variations to give dependable results. Hammett ('25) concluded that bone length in rats is little affected by systemic deprivation. The same author ('26) found bone growth in length related to body growth in length. Donaldson ('19) considers length of rat leg bones to be related to body length as well as to weight.

Evidence obtained from a study of skeletal dimensions of several forms has disclosed a high degree of correlation between various bones as well as between bone length and body weight. Castle ('22) concluded on the basis of these high correlations that factors influencing size in rabbits were, for the most part, general in their action. Kopeć ('27) expressed the view that in fowls some factors were general while others were local.

Body length and tail length in our study were measured to the nearest millimeter by the method described by Sumner

('27). Body length by this method is the total length less the tail length. Relative tail length was obtained to the nearest per cent by dividing the tail length by the total length.

When counting the number of caudal vertebrae, the second vertebra showing complete chevron ossicles was taken as number 1. Although a hand lens was used, it was sometimes difficult to determine whether or not the terminal vertebra was present. Thus, the number of caudal vertebrae is not, in any study, as exact a criterion as might be desired.

For the study of growth rates, observations were made the first day and every second day thereafter until the thirty-first day. From the thirty-first to the 181st day weights were taken every tenth day. The highest figure recorded for each mouse was considered its adult weight.

Our skeletal measurements were like those described by Saller ('25) and taken to the nearest 0.01 mm. by means of a Starrett bench micrometer. The humerus, femur, and tibia selected for measurement were always the right.

Skull length is taken as the distance from the highest point of the foramen magnum to the most anterior surface of the incisor teeth. Howell ('24) considered condylo-basilar length (a very similar measurement) the most satisfactory criterion for the arrangement of a series of *Microtus* skulls with respect to their general development.

Our skull width is Saller's 'Kleinste Stirnbreite.' He describes it as the "width of the frontal bones between the points of their strongest lateral constrictions on the temporal lines." However, in our mice, this narrowest width seems to be posterior to the lineae temporales.

Humerus length is taken as the distance from the highest point of the caput humeri to the most distal point of the external side wall of the trochlea.

Femur length is measured from the highest point of the trochanter major to the deepest point of the condylus internus. In a number of our examples the distal end of the femur seemed to be abnormally bent. None so affected was included in the computations.

Tibia length is taken as the distance from the most proximal point of the articulation surface to the most distal point on the malleolus medialis.

Since no animals of a lesser age than 180 days were included in the tabulations, it is probable that all characters used as size indices had attained their maximum development. Latimer ('27) found that leg and wing bones of fowls had obtained complete length a considerable time before maturity.

All bones were cleaned after boiling in a solution of water, ammonia, and phenol. They were allowed to dry at least two days in the open air before being measured. The variations in time before measurement cannot greatly have altered the values. Donaldson ('19) found that freshly cleaned rat bones changed in length less than 1 per cent after being oven-dried at 96°C. for six days. This treatment demonstrates that even complete desiccation has almost no effect on bone length.

The bearing of young may cause an increase in the body weight of the female, so in the study of adult weight parous and nulliparous females are treated separately. Watson ('05) observed this effect in rats, although his numbers were too few to be conclusive.

A factor which might conceivably affect the final size is the number of young in the litter. It is well known that individuals from large litters are smaller at birth than newborn young from small litters. It is generally conceded, however, that the effect of differential litter size is soon lost. Castle ('22) concluded that ultimate size in rabbits is little affected, if at all, by size at weaning. Punnett and Bailey ('18) remarked that litter size has no bearing on the adult size of rabbits. MacDowell ('14) was in perfect agreement. Wright ('22) held that adult weight in guinea-pigs is determined by the young themselves. Extrinsic factors such as litter size play no part. In rats, Livesay ('30) found that the influence of litter size on weight is lost at as early an age as ninety days.

In order to determine whether litter size has had any effect on the adult size of mice, coefficients of correlation for litter size and adult weight and for litter size and skull length were computed for both sexes of pure musculus and the F_1 hybrids. These eight values are shown in table 1. In three cases there does appear to be a doubtfully significant slight negative correlation between litter size and final size, indicating that the early influence of litter size may not have been entirely lost. These results are not consistent, however, since in two instances the correlation is slightly positive and

TABLE 1
Correlations for size of litter and adult size

	MALES		FEMALES	
	Number of animals		Number of animals	
Litter size and adult weight				
Musculus ♀ × musculus ♂	27	$r = -.34 \pm .114$	26	$r = +.02 \pm .196^1$
Musculus ♀ × bactrianus ♂	37	$r = -.21 \pm .108$	29	$r = -.24 \pm .115^2$
Litter size and skull length				
Musculus ♀ × musculus ♂	65	$r = -.25 \pm .078$	82	$r = +.11 \pm .074$
Musculus ♀ × bactrianus ♂	35	$r = -.32 \pm .102$	36	$r = -.20 \pm .112$

¹ Nulliparous. ² Parous.

in no case is the negative correlation very convincing. The probability, then, is that in mice, as in rabbits, guinea-pigs, and rats, the effects of litter size on physical dimensions are lost before maturity.

ANALYSIS OF DATA

Mean body measurements (in millimeters) for the P_1 , the F_1 , and the back-cross mice (in the production of which only F_1 's from musculus females were employed) are given in table 2. In body length the F_1 animals are intermediate, although nearer the larger race. The smaller size of the female F_1 hybrids when the mother was bactrianus (B) seems difficult to explain, since the males were slightly—though not signifi-

cantly—longer than in the reciprocal cross. The back-cross individuals from both types of matings are, on the whole, intermediate between the F_1 and parental generations in the matter of body length. In the females the body length is slightly less when the mother was a hybrid. This is probably a chance deviation, since the means for the males of the two types are exactly the same.

For mean tail lengths again the F_1 values are intermediate between the parental means, while the back-cross means lie between those of the F_1 and the musculus. Here, however, the differences between the reciprocal F_1 and back-cross matings are statistically insignificant.

Relative tail lengths (means) have the same order as the absolute values. In the females, however, the musculus (M) are proportionately shorter-tailed and have approximately the same values as the F_1 females. One type of back-cross mating ($F_1 \text{♀} \times M \text{♂}$) shows a relatively longer tail than the reciprocal. This difference, although statistically significant (0.9 ± 0.16 per cent), is probably of no great importance.

In number of caudal vertebrae the six matings retain their characteristic positions. The F_1 's are intermediate between the two parent species, while the back-cross animals are between the F_1 and the musculus parent. This character clearly demonstrates blending inheritance.

In the same table adult weights are presented. The F_1 means are intermediate between those of the parent races, while the back-cross means are between those for F_1 and pure musculus. The reciprocal F_1 's show significant differences neither in the males nor in the females (nulliparous). The two types of back-cross matings likewise produce no significant differences in the mean weights. The females from bactrianus $\text{♀} \times$ bactrianus ♂ and musculus $\text{♀} \times$ bactrianus ♂ matings consist of two classes, parous and nulliparous. The increased weights (none of which were recorded less than ten days before the birth of a litter) of the parous females probably is due less to the effects of motherhood than to selection which may have occurred. The bactrianus females, par-

TABLE 2

Comparative body measurements of the bactrianus (B) and musculus (M) races and of their F₁ and back-cross hybrids

MATING	BODY LENGTH (MM.)			TAIL LENGTH (MM.)			RELATIVE TAIL LENGTH (PER CENT)				CAUDAL VERTEBRAE (NUMBER)				ADULT WEIGHT (GRAMS)						
	♂ ♂		♀ ♀	♂ ♂		♀ ♀	♂ ♂		♀ ♀	♂ ♂		♀ ♀	♂ ♂		♀ ♀	♂ ♂		♀ ♀			
	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean			
B ♂ × B ♂	17	80.2 ± .51	26	79.7 ± .49	12	68.8 ± 1.22	21	67.7 ± .53	12	45.8 ± .45	21	46.0 ± .18	37	20.1 ± .06	19	15.5 ± .17	14	12.8 ± .23	(P) ¹		
M ♀ × M ♂	72	95.8 ± .23	56	98.3 ± .50	63	93.7 ± .24	56	92.0 ± .38	63	49.5 ± .07	56	48.4 ± .10	65	25.0 ± .04	27	31.4 ± .49	25	29.4 ± .74	(NP) ²		
M ♂ × B ♂	39	90.8 ± .40	36	91.3 ± .45	32	85.7 ± .37	32	85.0 ± .44	32	48.6 ± .15	32	48.3 ± .13	34	23.1 ± .07	46	22.8 ± .07	37	22.0 ± .32	16	18.3 ± .36	(NP)
B ♀ × M ♂	14	91.1 ± .52	17	85.2 ± .65	12	83.6 ± .92	12	80.9 ± .91	12	47.7 ± .17	16	48.6 ± .21	15	22.6 ± .09	17	22.8 ± .08	14	23.3 ± .53	20	17.3 ± .41	
M ♀ × F ₁ ♂	71	93.8 ± .37	70	93.7 ± .33	70	89.5 ± .43	66	87.2 ± .40	70	48.3 ± .09	66	48.1 ± .12	74	23.9 ± .05	65	27.0 ± .32	61	26.3 ± .49			
F ₁ ♀ × M ♂	74	93.8 ± .28	69	91.0 ± .27	71	90.2 ± .42	62	87.8 ± .38	71	49.0 ± .10	62	49.0 ± .10	98	23.8 ± .04	79	24.1 ± .05	69	28.5 ± .42	68	24.8 ± .39	

¹ P = parous.

² NP = nulliparous.

TABLE 3

Comparative skeletal measurements of the bactrianus (B) and musculus (M) races and of their F₁ and back-cross hybrids

MATING	SKULL LENGTH (MM.)			SKULL WIDTH (MM.)			HUMERUS LENGTH (MM.)			FEMUR LENGTH (MM.)			TIBIA LENGTH (MM.)						
	♂♂	♀♀		♂♂	♀♀		♂♂	♀♀		♂♂	♀♀		♂♂	♀♀					
		Number	Mean		Number	Mean		Number	Mean		Number	Mean		Number	Mean	Number	Mean		
B ♂ × B ♂	17	20.48 ± .074	26	22	3.87 ± .025	30	3.93 ± .014	19	10.44 ± .054	29	10.23 ± .044	20	13.67 ± .090	29	13.56 ± .108	20	15.22 ± .094	31	15.07 ± .087
M ♂ × M ♂	65	21.71 ± .033	83	70	4.30 ± .006	98	4.39 ± .012	67	11.37 ± .020	90	11.30 ± .026	60	14.21 ± .035	88	14.75 ± .049	67	16.53 ± .039	94	16.62 ± .048
M ♀ × B ♂	39	21.98 ± .040	37	39	3.99 ± .011	40	4.12 ± .013	39	11.25 ± .029	40	11.00 ± .034	39	14.67 ± .044	34	14.79 ± .063	38	16.50 ± .114	15	15.88 ± .137
B ♂ × M ♂	13	22.00 ± .070	16	13	4.05 ± .010	16	3.99 ± .021	12	11.24 ± .066	15	10.69 ± .070	10	14.66 ± .137	9	14.29 ± .062	13	16.50 ± .114	15	15.88 ± .137
M ♀ × F ₁ ♂	70	21.96 ± .042	66	71	4.09 ± .013	67	4.18 ± .011	70	11.53 ± .037	65	11.15 ± .040	63	14.69 ± .060	52	14.69 ± .059	71	16.78 ± .062	66	16.60 ± .057
F ₁ ♀ × M ♂	71	22.01 ± .042	65	73	4.14 ± .012	67	4.09 ± .010	72	11.46 ± .033	64	11.03 ± .026	67	14.68 ± .047	56	14.48 ± .047	69	16.95 ± .051	66	16.61 ± .051

ticularly, are late breeders and it seems likely that the larger females bred before the age of six months, while the smaller ones did not. Thus, the true mean for all females, had they been allowed to remain virgin, probably would lie between the values given. The difference existing in the F_1 females is more difficult to explain plausibly, since all females not used as breeders were kept separated from the males. This difference, although less than that in the pure bactrianus animals, probably can, at least partly, be attributed to unintentional selection.

In table 3, showing skeletal measurements, skull length presents a quite different picture. In the males the F_1 and back-cross values are approximately equal and both significantly exceed the larger parent. In the females the F_1 's from musculus mothers surpass the pure musculus, although the difference is scarcely significant statistically (0.17 ± 0.075 mm.). The mean skull length for females of the reciprocal cross is much less, intermediate between the two parental species, but nearer the larger. The back-cross females are not significantly different from the musculus.

Heterosis is exhibited to a marked degree in the F_1 animals, particularly in the progeny of musculus mothers. Females from the reciprocal mating are too few in number to make their lower average of much critical significance. Contrary to the usual results in mammalian crosses, heterosis appears still to have retained much of its force in the back-cross.

Heterosis seems to be little if at all manifested in the matter of skull width. The F_1 males are intermediate, while the back-cross means lie between the F_1 and the musculus values. A like situation prevails among the females excepting that the back-cross mice from hybrid mothers have slightly narrower skulls than F_1 's from musculus mothers (4.09 and 4.12 mm., respectively). The reciprocal crosses in both F_1 and back-cross matings exhibit differences. These, however, are not consistent. F_1 males from musculus $\times$ bactrianus crosses have narrower skulls than reciprocal F_1 males. In the females, conditions are reversed. Back-cross

males from hybrid mothers have broader skulls than those from musculus mothers, while females have narrower. The deviations are not great and probably merely fortuitous.

Table 3 likewise shows mean humerus lengths for the six types of matings. Again the F_1 animals of both sexes are intermediate, but approach more closely the larger parent. Back-cross animals of both sexes have longer humeri than the F_1 's, those of the males exceeding even the musculus. The values for the two types of back-crosses do not differ significantly.

In the matter of femur length, heterosis is again more evident. Males of the two F_1 and the two back-cross matings have nearly identical femur lengths. These figures so far exceed those for musculus ♀ × musculus ♂ males that the differences are unquestionably significant. The difference between the mean femur lengths of F_1 males (musculus ♀ × bactrianus ♂) and pure musculus males is 0.46 ± 0.056 mm.; that between back-cross males whose mothers were musculus and straight musculus males is 0.48 ± 0.069 mm. The reciprocal back-cross and pure musculus males show a difference of 0.47 ± 0.059 mm.

Females of reciprocal crosses of both F_1 and back-cross generations show different results. With musculus mothers, first-generation and back-cross hybrids do not significantly differ from pure musculus. Reciprocal F_1 's have a lower value, but since the mean was based on only nine animals, little reliance can be placed in it. The difference between the two back-cross matings is 0.21 ± 0.075 mm., so is of border-line significance only.

Tibia lengths present a situation similar to that in the humeri. The means of F_1 males are nearly identical with that of the musculus parent, while the back-cross males of both types of matings considerably exceed it. In the females the F_1 animals from musculus mothers have a mean value slightly less than that of pure musculus, while those of the back-cross females approximately equal it. The reciprocal F_1 females, based on only fifteen observations, have a mean tibia length intermediate between the two parents.

TABLE 4
Coefficients of variation in races of bactrianus and musculus mice and in their F₁ and back-cross hybrids

MATING	BODY LENGTH		TAIL LENGTH		RELATIVE TAIL LENGTH		CAUDAL VERTEBRAE		ADULT WEIGHT		SKULL LENGTH		SKULL WIDTH		HUMERUS LENGTH		FEMUR LENGTH		TIBIA LENGTH	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀
B ♀ × B ♂	3.38	4.68	9.08	5.36	5.03	2.68	3.30	3.27	7.27	10.16	2.21	2.32	4.49	2.94	3.32	3.41	4.35	6.33	4.08	4.77
M ♀ × M ♂	3.07	5.64	2.99	4.63	1.68	2.20	1.64	2.34	12.20	19.12	1.79	2.88	1.15	2.91	2.19	3.21	2.86	4.53	2.87	4.13
M ♀ × B ♂	4.07	4.38	3.67	4.34	2.66	2.31	2.52	2.88	12.94	11.53	1.70	2.42	2.63	2.96	2.35	2.85	2.79	3.69	2.76	2.80
B ♀ × M ♂	3.17	4.66	5.66	6.66	1.78	2.52	2.17	2.25	12.73	16.77	1.70	2.47	1.33	3.13	3.03	3.75	4.39	1.92	3.71	4.98
M ♀ × F ₁ ♂	4.86	4.30	5.88	5.50	2.39	3.02	2.81	2.56	13.90	21.62	2.39	2.48	3.84	3.29	4.00	4.25	4.79	4.29	4.58	4.14
F ₁ ♀ × M ♂	3.81	3.72	5.83	5.04	2.56	2.35	2.68	2.71	18.01	18.99	2.38	1.78	3.65	3.03	3.63	2.81	3.90	3.61	3.71	3.69

In table 4 are listed the coefficients of variation for the ten quantitative characters studied. In every character, excepting adult weight, musculus males are less variable than bactrianus males. The musculus females are likewise less variable than those of bactrianus, the only exceptions being in adult weight, body length, and skull length.

Coefficients of variation for the F_1 males from musculus ♀ $\times$ bactrianus ♂ matings are intermediate between the coefficients for the males of the two parent species in five characters; they exceed either parent in two characters and are less than either in three. Females are intermediate in variability in six characters, greater in one, and less in three.

The reciprocal F_1 animals reveal a similar situation. The coefficients of variation for males are intermediate in position in six characters, greater in two, and less in two. Females are more variable in four characters, less in three, and intermediate in three.

Back-cross males from $M \text{♀} \times F_1 \text{♂}$ matings are more variable than F_1 males ($M \text{♀} \times B \text{♂}$) in all quantitative indices excepting relative tail length; the females likewise are more variable in the majority of characters, the only exceptions being body length and number of caudal vertebrae. The males in the reciprocal back-cross are also more variable than the F_1 males in all characters excepting body length and relative tail length, while the females show greater variability in five characters and lesser in the remaining five than do the F_1 females.

In comparing the variability of the back-cross generation ($M \text{♀} \times F_1 \text{♂}$) with the parental species, we find the males more variable than males of either parent form in six characters and intermediate between them in the other four. The females show greater variability in five measurements, are intermediate in three, and less in two.

The second type of back-cross matings seems to have produced slightly less variable offspring. In four measurements the coefficients of variation of the males exceed those of the parental species of the same sex, while in six the values are

intermediate. In the opposite sex only one measurement exhibits greater variability than those for the parental females, while four show intermediate and five, lesser variability.

Thus, the coefficients of variation for ten quantitative indices show the pure musculus mice, as would be expected from the degree of inbreeding they have undergone, to be less variable than pure bactrianus. The F_1 animals, on the whole, are intermediate between the two species, while the back-cross generations indicate a markedly greater variability than the F_1 's. These findings are in line with the multiple-factor explanation for size inheritance.

Although the mean values of the size indices when not too greatly augmented by hybrid vigor show the F_1 animals to be intermediate between the two parent races, thus indicating blending inheritance and multiple factors, an alternative explanation is possible. Davenport ('17) considered that factors for tallness in humans were mostly recessive and Lindstrom ('26) found that small fruit size in certain strains of tomatoes was at least partially dominant over large size, so it may be that small size in mice is, in reality, dominant. The influence of heterosis might then be responsible for bringing the genotypically small mice into phenotypical intermediates. If true, such a condition should be disclosed by the back-cross, since the influence of heterosis theoretically is largely lost in that generation.

Were one major recessive size factor chiefly responsible for the genetic quantitative differences in our two species of mice, the genetically small heterozygous F_1 's when crossed to the homozygous recessive large species should produce offspring of two kinds, heterozygous small mice and homozygous large mice, in equal numbers. Even though there were lesser modifying factors without dominance affecting size, the back-cross curves of adult size characters nevertheless should be distinctly bimodal. A perusal of the tabulated data shows this not to be the case.

In order to make the situation more evident, sixteen frequency polygons were constructed. These are shown in figures 1 to 4. The characters selected as representative are body length, adult weight, skull length, and humerus length of males. Since the mean values of the two types of back-cross matings have been shown not to differ markedly, the combined data were used.

Figure 1 shows the distribution of the body lengths among the back-cross males as well as among the two parent strains and the F_1 generation (*musculus* ♀ × *bactrianus* ♂). Figure 2 shows adult weights for the same four classes; figure 3 gives skull lengths and 4 presents humerus lengths. It can easily be seen that there is little semblance to bimodalism in the back-cross frequency polygons. It is highly improbable, therefore, that a single recessive factor is responsible for the large size of *Mus musculus*.

Even though the general intermediate position of our mice, together with the increase in variability of the back-cross generation, indicates the applicability of the multiple-factor theory to size inheritance, the matter cannot be regarded as satisfactorily proved until linkage between quantitative characters and some freely mendelizing qualitative factor is demonstrated. If such linkage be present in our investigation, an analysis of the back-cross matings may detect it.

In order to find out whether there has been any tendency for the larger size of the parent, recessive for three qualitative characters, to remain associated with the recessive characters, animals of the back-cross matings, treating each type separately, have been divided into dominants and recessives, considering only one pair of allelomorphs at a time. Thus all males of the back-cross matings, *musculus* ♀ × F_1 ♂, carrying the dominant agouti factor A^w have been compared with all non-agouti males with the gene a . In like manner the blacks (B) and browns (b) and the intense (D) and dilutes (d) have been compared. The same procedure has been carried out for the females and for both sexes of the reciprocal back-cross mating.

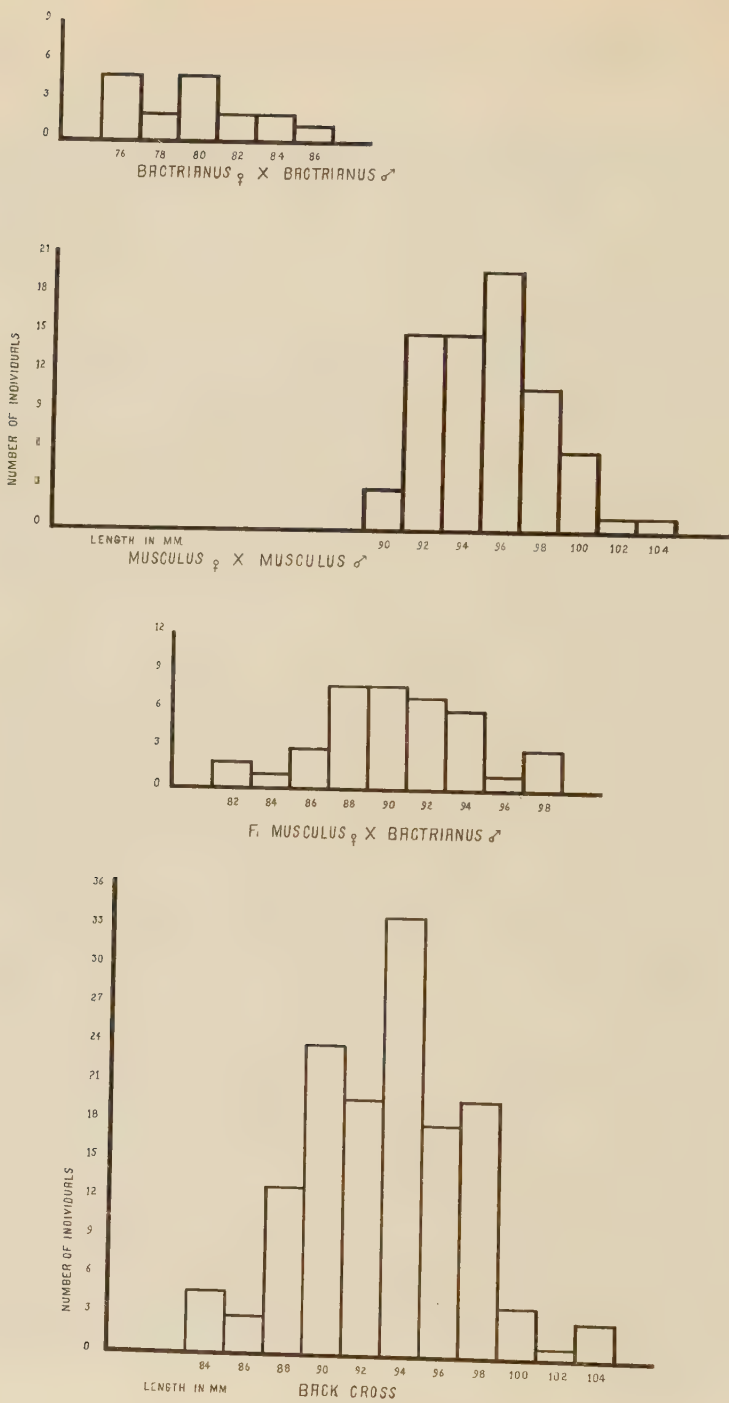


Fig. 1 Body length. Males.

The back-cross animals from musculus females are shown in tables 5 and 6.

In body length the three recessive classes exceed their dominant allelomorphs in all cases excepting one. Agouti males are longer than non-agoutis. In tail length agouti males and females and black females exceed their allelo-

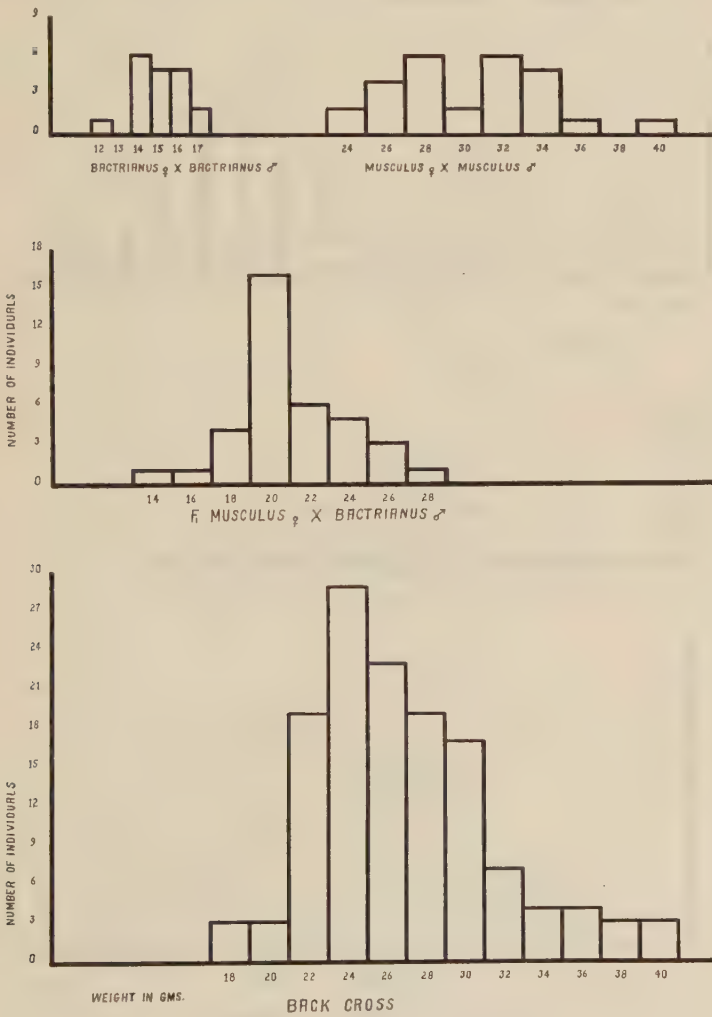


Fig. 2 Adult weight. Males.

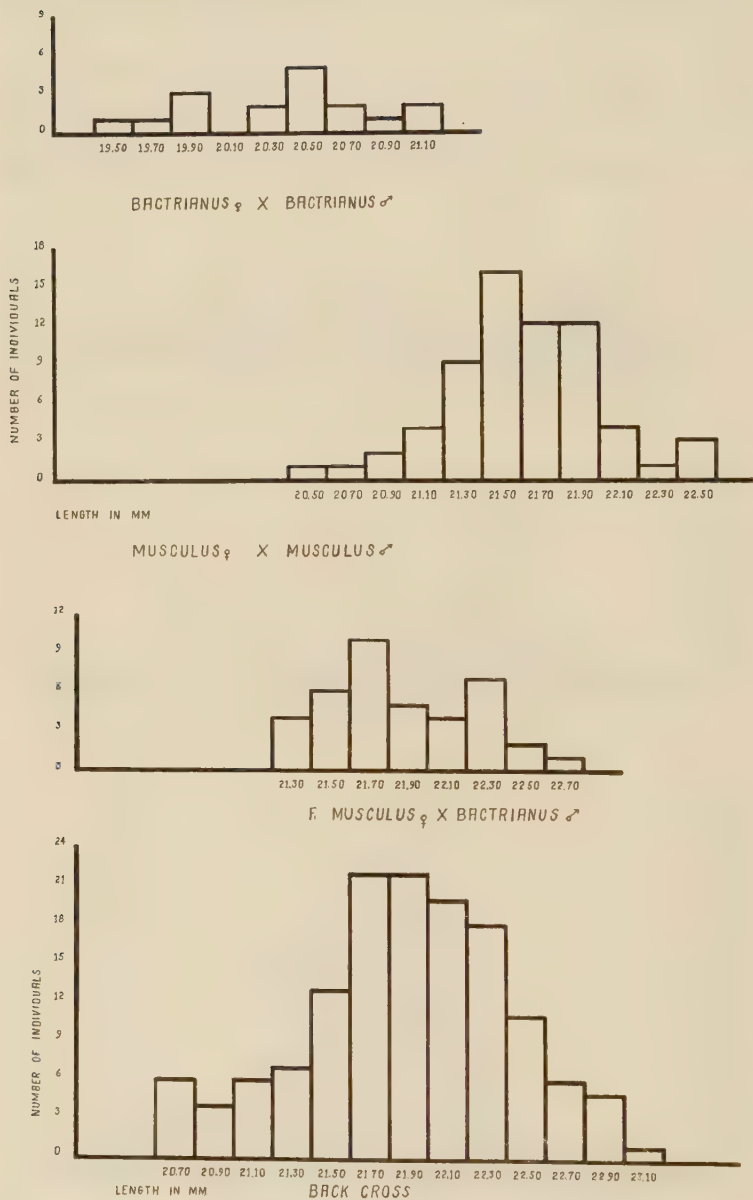


Fig. 3 Skull length. Males.

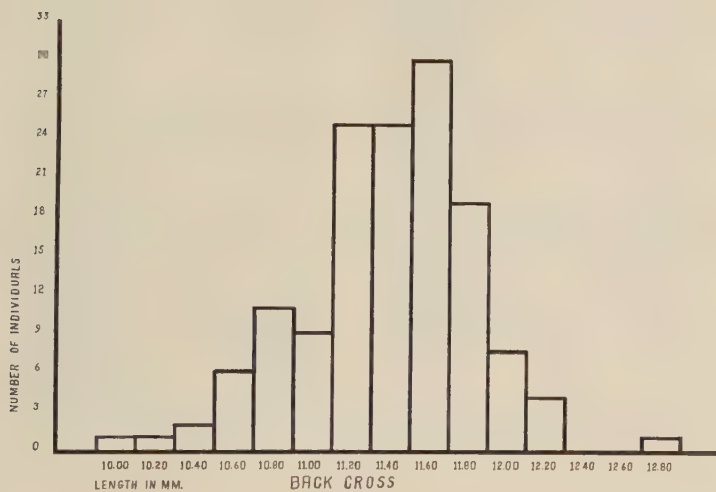
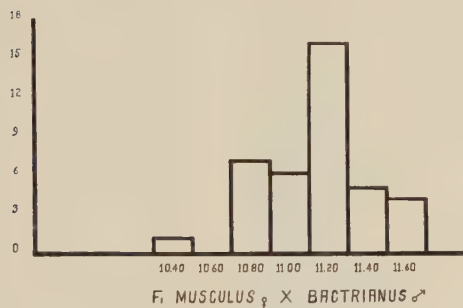
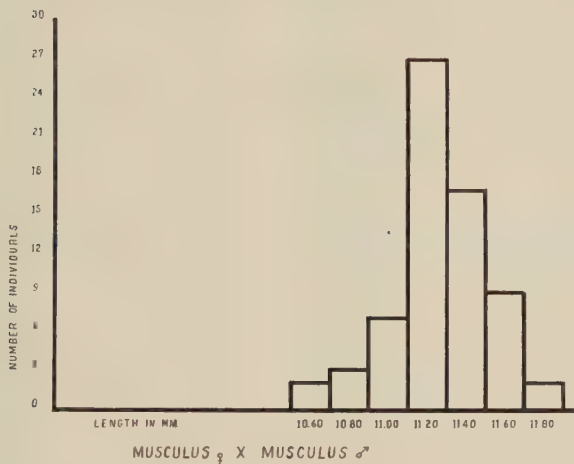
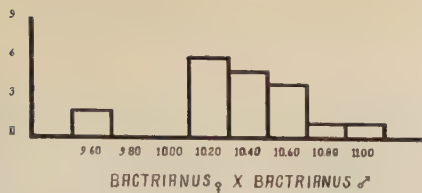


Fig. 4 Humerus length. Males.

TABLE 5
Comparative body measurements of different phenotypic classes of back-cross mice from matings, $M\varnothing \times F_1\delta$

PHENO- TYPE	BODY LENGTH (MM.)			TAIL LENGTH (MM.)			RELATIVE TAIL LENGTH (PER CENT)			CAUDAL VERTEBRAE (NUMBER)			ADULT WEIGHT (GRAMS)					
	$\delta\delta$	Mean	Number	$\varnothing\varnothing$	Mean	Number	$\delta\delta$	Mean	Number	$\varnothing\varnothing$	Mean	Number	$\delta\delta$	Mean	Number			
A ^w	39	94.4 ± .47	33	93.2 ± .42	38	90.0 ± .52	32	87.5 ± .64	38	48.3 ± .12	32	48.3 ± .15	40	23.8 ± .07	34	26.9 ± .38	29	24.5 ± .54
a	32	93.0 ± .56	37	94.2 ± .48	32	89.0 ± .69	34	86.3 ± .48	32	48.9 ± .15	34	47.9 ± .18	34	23.9 ± .08	31	27.1 ± .51	32	28.0 ± .74
B	35	92.4 ± .48	31	92.3 ± .49	34	88.7 ± .63	30	87.4 ± .61	34	49.0 ± .16	30	48.6 ± .14	34	23.8 ± .09	33	26.5 ± .41	28	25.1 ± .58
b	36	95.1 ± .51	39	94.8 ± .40	36	90.3 ± .56	36	86.9 ± .52	36	48.7 ± .10	36	47.7 ± .17	40	23.9 ± .06	34	23.9 ± .07	32	26.5 ± .46
D	38	93.7 ± .50	30	93.2 ± .50	37	88.9 ± .59	28	86.5 ± .51	37	48.6 ± .13	28	48.0 ± .16	34	23.6 ± .08	33	27.0 ± .53	35	26.8 ± .73
d	33	93.8 ± .54	40	94.1 ± .42	33	90.2 ± .60	38	87.6 ± .51	33	49.0 ± .14	38	48.2 ± .17	40	24.1 ± .06	32	27.5 ± .55	36	26.0 ± .66

TABLE 6
Comparative skeletal measurements of different phenotypic classes of back-cross mice from matings, $M\varnothing \times F_1\delta$

PHENO- TYPE	SKULL LENGTH (MM.)			SKULL WIDTH (MM.)			HUMERUS LENGTH (MM.)			FEMUR LENGTH (MM.)			TIBIA LENGTH (MM.)			
	♂ ♂ Number	Mean	♀ ♀ Number	♂ ♂ Number	Mean	♀ ♀ Number	♂ ♂ Number	Mean	♀ ♀ Number	♂ ♂ Number	Mean	♀ ♀ Number	♂ ♂ Number	Mean	♀ ♀ Number	
A ^w	39	22.00 ± .051	32	21.90 ± .061	39	4.12 ± .017	33	4.20 ± .014	38	11.61 ± .045	31	11.03 ± .069	36	14.81 ± .073	23	14.73 ± .098
a	31	21.30 ± .070	34	22.00 ± .067	32	4.06 ± .017	34	4.16 ± .015	34	11.43 ± .039	34	11.27 ± .038	27	14.55 ± .096	29	14.66 ± .071
B	35	21.85 ± .062	29	21.97 ± .075	35	4.07 ± .019	30	4.16 ± .015	34	11.41 ± .052	30	11.18 ± .045	30	14.61 ± .084	25	14.52 ± .097
b	35	22.07 ± .054	37	21.93 ± .055	36	4.11 ± .016	37	4.19 ± .016	36	11.59 ± .050	37	11.14 ± .061	33	14.77 ± .083	37	14.85 ± .063
D	37	21.84 ± .059	28	22.01 ± .074	37	4.10 ± .019	29	4.19 ± .019	37	11.50 ± .051	28	11.09 ± .063	34	14.68 ± .077	24	14.51 ± .105
d	33	22.09 ± .057	38	21.90 ± .056	34	4.08 ± .017	38	4.17 ± .015	33	11.56 ± .054	37	11.21 ± .050	29	14.71 ± .093	28	14.84 ± .056

morphs. Relative tail length and number of caudal vertebrae show little difference between the dominant and recessive classes.

The adult weight of intense females is greater than that of dilute, while the males of these two classes present identical means. In the other two pairs of allelomorphs the recessive animals of both sexes are heavier.

Skull length in agouti males and black and intense females is slightly greater than in their recessive companions. In the other three pairs recessive animals show greater length. The differences in skull width are all slight, the recessive exceeding in two pairs and the dominants in four.

In both humerus and femur length the recessive members of four pairs surpass their dominant allelomorphs, while in two the conditions are reversed. Tibia length reveals the same situation.

Mean values for the reciprocal back-cross are shown in tables 7 and 8.

In body length the recessive members of contrasting pairs exceed the dominants in every instance, while in tail length there is but one exception (agouti females). Tail length, expressed in per cent of total length, likewise shows but the one exception.

Recessive and dominant animals exhibit little difference in the number of caudal vertebrae. In two cases the mean values are equal, in three the recessives exceed, and in one the dominants.

In adult weight the black and brown females have identical means. The remaining five pairs, however, show the recessives to be heavier.

Both male and female agoutis have longer skulls than non-agoutis. Brown and dilute of both sexes, however, exceed their dominant allelomorphs. In skull width differences are very slight, with the dominant members exceeding the recessives in every pair excepting one.

Recessives surpass dominants in humerus length in four instances, equal them in one, and are slightly less in one. In

TABLE 7

Comparative body measurements of different phenotypic classes of back-cross mice from matings, $F_1 \text{♀} \times M \text{♂}$

PHENO- TYPE	BODY LENGTH (MM.)				TAIL LENGTH (MM.)				RELATIVE TAIL LENGTH (PER CENT)				CAUDAL VERTEBRAE (NUMBER)				ADULT WEIGHT (GRAMS)			
	♂		♀		♂		♀		♂		♀		♂		♀		♂		♀	
	Mean		Mean		Mean		Mean		Mean		Mean		Mean		Mean		Mean		Mean	
	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean
A ^w	33	92.9 ± .40	31	90.9 ± .44	32	88.0 ± .62	27	88.4 ± .56	32	48.6 ± .15	27	49.3 ± .14	44	23.8 ± .06	36	24.0 ± .07	31	27.0 ± .55	31	23.4 ± .39
a	41	94.4 ± .37	38	91.1 ± .37	39	92.1 ± .49	35	87.2 ± .51	39	49.4 ± .12	35	48.8 ± .13	54	23.8 ± .06	43	24.1 ± .07	38	30.0 ± .57	37	25.9 ± .59
B	25	93.0 ± .51	33	90.3 ± .41	25	89.7 ± .80	29	87.0 ± .47	25	49.0 ± .19	23	48.9 ± .14	43	23.8 ± .06	40	23.9 ± .08	33	27.7 ± .70	33	24.8 ± .62
b	49	94.2 ± .33	36	91.7 ± .38	46	90.5 ± .48	33	88.4 ± .57	46	49.1 ± .12	33	49.0 ± .14	55	23.8 ± .06	39	24.2 ± .06	46	29.1 ± .51	35	24.8 ± .47
D	38	93.1 ± .38	35	90.7 ± .44	37	89.3 ± .60	32	87.2 ± .52	37	48.9 ± .13	32	49.0 ± .13	51	23.8 ± .06	45	23.9 ± .07	35	28.6 ± .61	34	24.5 ± .55
d	36	94.5 ± .39	34	91.4 ± .36	34	91.2 ± .57	30	88.4 ± .54	34	49.2 ± .16	30	49.1 ± .14	47	23.7 ± .06	54	24.2 ± .07	34	28.7 ± .58	34	25.1 ± .54

TABLE 8

Comparative skeletal measurements of different phenotypic classes of back-cross mice from matings, $F_1 \text{♀} \times M \text{♂}$

PHENO- TYPE	SKULL LENGTH (MM.)				SKULL WIDTH (MM.)				HUMERUS LENGTH (MM.)				FEMUR LENGTH (MM.)				TIBIA LENGTH (MM.)			
	♂		♀		♂		♀		♂		♀		♂		♀		♂		♀	
	Mean		Mean		Mean		Mean		Mean		Mean		Mean		Mean		Mean		Mean	
	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Number	Mean
A ^w	33	22.02 ± .068	30	21.96 ± .049	33	1.15 ± .014	30	1.12 ± .013	32	11.38 ± .046	29	11.04 ± .042	30	14.60 ± .072	25	14.59 ± .076	32	16.92 ± .072	29	16.55 ± .087
a	38	22.00 ± .051	35	21.79 ± .042	40	1.13 ± .018	37	1.07 ± .015	40	11.52 ± .046	35	11.03 ± .032	37	14.75 ± .061	31	14.39 ± .057	37	16.97 ± .072	37	16.86 ± .060
B	24	21.90 ± .062	32	21.80 ± .039	24	1.15 ± .019	32	1.10 ± .014	24	11.37 ± .056	29	10.95 ± .031	23	14.55 ± .091	24	14.46 ± .064	23	16.85 ± .100	32	16.96 ± .064
b	47	22.04 ± .047	33	21.89 ± .051	49	1.13 ± .015	35	1.09 ± .014	48	11.50 ± .041	35	11.10 ± .038	44	14.75 ± .052	32	14.49 ± .067	46	17.00 ± .057	34	16.74 ± .075
D	36	21.88 ± .059	33	21.82 ± .045	38	1.15 ± .015	34	1.07 ± .017	38	11.33 ± .042	31	11.03 ± .031	37	14.61 ± .063	30	14.46 ± .073	35	16.70 ± .075	34	16.58 ± .077
d	35	22.16 ± .054	32	21.91 ± .047	35	1.13 ± .018	33	1.11 ± .011	34	11.57 ± .048	33	11.03 ± .040	30	14.78 ± .069	26	14.49 ± .057	34	17.21 ± .056	32	16.84 ± .065

femur length recessive values are greater in five pairs and less in one, while the mean tibia lengths of the recessives are greater without exception.

From these tables it is apparent that there has been a general tendency for those animals showing recessive qualitative characters to exceed their dominant allelomorphs in the quantitative indices investigated. Since this tendency seems to be manifested in all three allelomorphic pairs, a comparison of the extracted triple recessives with the triple dominants should be more effective in demonstrating linkage. These comparisons are given in table 9.

With the exception of the number of caudal vertebrae in which the means of the two classes are equal, the recessive males (dba) surpass the dominant males (DBA^w) in all characters excepting skull width. Here the difference is of no importance (0.03 ± 0.035 mm.). In body length, tail length, and humerus length the difference is more than three times its probable error, so can be considered as statistically significant. The recessive females likewise significantly exceed the dominant in three characters: body length, adult weight, and humerus length. In four other characters the difference in favor of the recessives is not significant, while in the remaining three dimensions the dominant animals slightly exceed. Although the number of individuals in both classes is small, the fact, that for six quantitative indices the means of the extracted musculus type animals are significantly greater than those of the bactrianus type back-cross individuals, is strongly indicative of linkage between qualitative and quantitative characters. That this larger size of the dilute brown non-agoutis is genetic and not physiologic is demonstrated by the occurrence of large races of intense black agouti mice.

TABLE 9
Extracted parental types from back-cross generation

CHARACTER	♂				♀					
	Number	(DBA ^w)	Number	(dba)	Difference	Number	(DBA ^w)	Number	(dba)	Difference
Body length (mm.)	16	92.1 ± .58	19	95.1 ± .66	3.0 ± .88	15	91.6 ± .69	27	94.2 ± .49	2.6 ± .85
Tail length (mm.)	15	87.3 ± 1.10	18	91.5 ± .82	4.2 ± 1.37	14	87.2 ± .72	23	87.8 ± .70	.6 ± 1.00
Tail length (per cent)	15	48.5 ± .27	18	49.1 ± .17	.6 ± .32	14	48.7 ± .17	23	48.1 ± .27	-.6 ± .32
Caudal vertebrae	19	23.8 ± .10	25	23.8 ± .08	.0 ± .13	19	23.8 ± .10	22	24.1 ± .06	.3 ± .12
Adult weight (grams)	14	27.4 ± .76	19	29.1 ± .83	1.7 ± 1.13	15	23.1 ± .54	25	26.7 ± .67	3.6 ± .86
Skull length (mm.)	16	21.83 ± .087	19	22.14 ± .068	.31 ± .110	14	22.02 ± .077	25	21.99 ± .060	-.03 ± .097
Skull width (mm.)	16	4.15 ± .026	20	4.12 ± .023	-.03 ± .035	15	4.15 ± .022	26	4.11 ± .018	-.04 ± .028
Humerus length (mm.)	16	11.40 ± .063	20	11.72 ± .073	.32 ± .096	13	11.05 ± .063	26	11.28 ± .041	.23 ± .075
Femur length (mm.)	16	14.66 ± .115	17	14.93 ± .097	.27 ± .150	11	14.60 ± .149	21	14.72 ± .067	.12 ± .163
Tibia length (mm.)	16	16.79 ± .122	20	16.92 ± .168	.13 ± .208	14	16.48 ± .150	25	16.79 ± .079	.31 ± .169

SUMMARY

The study of size inheritance in this mouse interspecific cross has shown it generally to be of the blending type with an increase in variability of the back-cross over the F_1 generation. In addition, there is strong indication that certain genetic factors productive of a large final size are found in the three chromosomes of the *Mus musculus* parent carrying the genes *d*, *b*, and *a*. In order to demonstrate this linkage conclusively, however, many more back-cross mice, especially of the two parental types, will be needed, so further work is underway. A survey of the whole makes it appear probable that size in mice is due to a number of chromosomal genes, most, but not all, of which are general in their action. The differences in behavior of the various skeletal measurements suggest the existence of certain local factors.

NOTE. List of literature cited will be found in succeeding paper.

